

NEW DATA ON THE ANKYLOSAURIAN DINOSAUR FROM THE LATE CRETACEOUS OF THE ANTARCTIC PENINSULA

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Ankylosaurian remains have been found in the Late Cretaceous (Campanian) of the Antarctic Peninsula (James Ross Island). The material includes a lower jaw, teeth, cervical, dorsal, sacral? and caudal vertebrae, ribs, parts of the scapula and ilium, autopodial bones, and armour from a single small individual. The Antarctic ankylosaur is probably a nodosaurid, based on the tooth form. The fragmentary material doesn't permit accurate identification at the generic or specific levels, so the specimens are referred to Nodosauridae indet. Current data on ankylosaurian distribution supports the hypothesis of a late dispersal of nodosaurids from the northern hemisphere to the Antarctic Peninsula via South America, although an early migration during Late Jurassic or Early Cretaceous time is possible. The Antarctic ankylosaur was small and lived in a high-latitude, although rather mild climate. □
Dinosauria, Ankylosauria, Late Cretaceous, Antarctic Peninsula, Gondwana, palaeobiogeography.

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In January 1986, ankylosaurian remains were recovered during fieldwork by the Instituto Antártico Argentino in Late Cretaceous (Campanian) sediments of James Ross Island, north-east of the Antarctic Peninsula (Gasparini et al., 1987). This was the first dinosaur to be discovered on the Antarctic continent (Olivero et al., 1991). Subsequently, other dinosaur remains have been collected from the Late Cretaceous of the Antarctic Peninsula, including a hypsilophodont ornithopod from the Campanian or Maastrichtian of Seymour Island (Hooker et al., 1991; Milner et al., 1992) and a theropod from the Coniacian or Santonian of James Ross Island (Molnar et al., this volume). Other occurrences of dinosaurs in Antarctica include a large crested theropod, *Cryolophosaurus ellioti*, and a *Plateosaurus*-like prosauropod from the Lower Jurassic of Mount Kirkpatrick, nearer the South Pole (Hammer & Hickerson, 1994).

A preliminary description of the ankylosaurian material and a discussion of its palaeobiogeographical implications were given by Gasparini et al. (1987) and Olivero et al. (1991). As a result of the preparation of the matrix in which the fossils were imbedded, two additional teeth were found. A latex cast was made from a mould of three articulated cervical vertebrae. Other material not described in the first account

includes parts of the scapula and ilium, vertebral pieces, metapodials and phalanges. In this paper, we discuss the affinities of the Antarctic ankylosaur in the light of the known material. New palaeobiogeographical data allow us to comment further on ankylosaurian distribution during the Late Cretaceous.

GEOGRAPHICAL AND GEOLOGICAL FRAMEWORK

The ankylosaurian material was discovered by the Argentinian geologists E. Olivero and R. Scasso about 2km inside Santa Marta Cove, in the north of James Ross Island (Olivero et al., 1991). The remains come from the Gamma Member of the Santa Marta Formation, in the lowermost part of the Marambio Group (Gasparini et al., 1987). They were recovered from locality D6-1, about 90m above the base of the Gamma Member. The lithology consists of massive green silty sandstones with abundant trace fossils. The ankylosaurian bones were associated with fish vertebrae and marine invertebrates, including bivalves, gastropods and nautiloid cephalopods (e.g., *Cymatoceras*). The unusual association of nautiloid phragmocones with the vertebrate bones could be explained as the result of stranding of shells along a beach (Woodburne & Zinsmeister, 1984). The ammonite assemblages

found above and below the dinosaur beds suggest a probably Late Campanian age (Olivero et al., 1991; Olivero, 1992).

The ankylosaurian remains could belong to a single specimen, as previously reported, although size differences between the bones suggest the possibility of two distinct individuals. The fossils were recovered from a small area about 6 meters square (Olivero et al., 1991). Most bones are fragmentary and have been much shattered by frost action. Preparation of the remains was carried out in the laboratory of the Museo de La Plata using mechanical techniques.

Collection designations. MLP, Museo de La Plata, La Plata; QM, Queensland Museum, Brisbane; ROM, Royal Ontario Museum, Toronto.

SYSTEMATIC PALAEOLOGY

Subclass DINOSAURIA Owen, 1842

Order ORNITHISCHIA Seeley, 1888

Suborder ANKYLOSAURIA Osborn, 1923

Family NODOSAURIDAE Marsh, 1890

Genus and species indet.

MATERIAL EXAMINED. A partial lower jaw with a tooth in situ, two isolated teeth, a cervical vertebra and a latex cast prepared from a natural mould of three articulated cervical vertebrae, two dorsal centra from the presacral rod, parts of the ?sacrum, three fragmentary caudal vertebrae, rib fragments, a fragmentary scapula, a fragment of ilium, four metapodials and two phalanges, and a collection of dermal elements, representing five different kinds of armour. All the remains are kept at the Departamento de Paleontología de Vertebrados, Museo de La Plata with the registration number MLP 86-X-28-1.

PROVENANCE AND AGE. Santa Marta Cove, northern James Ross Island, northeast of the Antarctic Peninsula; locality D6-1, lower section of the Gamma Member, Santa Marta Formation, Marambio Group; Late Cretaceous, Upper Campanian (Gasparini et al., 1987; Olivero et al., 1991; Olivero, 1992).

DESCRIPTION

A preliminary description of the specimens was given by Gasparini et al. (1987) and Olivero et al. (1991). Here we describe for the first time additional bones, including teeth, vertebrae, parts of the pectoral and pelvic girdles, and autopodial elements. Because the only other reasonably well known ankylosaur from the southern hemisphere is the specimen of *Minmi* described in this volume (QM F18101), detailed comparison will be made where possible with that specimen.

Lower jaw (Fig. 11-J). The only preserved portion of the lower jaw is a section of the left dentary,

including the sides and upper margin, but lacking the ventral margin (Gasparini et al., 1987). Nine alveoli are visible, including the foramina for tooth emplacement on the lingual side. The anterior and posterior parts of the tooth row are missing. The specimen is about 15mm thick and about 60mm long, as preserved. In occlusal view, the tooth row is slightly curved. One replacement tooth remains in place in the fifth preserved alveolus. The crown is broken but it looks like those of two isolated teeth described below. The dentary is a thick bone, as usual in ankylosaurs (Galton, 1983). It bears no armour. Four foramina are present on the labial side of the dentary. Medially, the splenial is missing and so the Meckelian canal is open. The lack of fusion of the splenial suggests that the lower jaw does not belong to a fully grown ankylosaur.

Teeth (Fig. 1A-H). In addition to the tooth preserved in situ in the lower jaw, there are two isolated teeth. Both teeth retain the crown and part of the root. The maximum crown width is about 7mm and the crown height about 7.5mm. As preserved, the more complete tooth is 20mm high. The teeth are typically ankylosaurian, with a leaf-shaped, laterally compressed crown (Coombs, 1990). They bear seven or eight denticles on the anterior margin and five on the posterior, each row of denticles separated from the other by a small apical cusp. The teeth are of about the same size as those of *Minmi* (QM F18101), but in *Minmi* the crowns are relatively higher (7.5 × 6mm rather than 7.5 × 7mm) and only have five or six anterior and three posterior denticles. A prominent, rugose basal cingulum is visible on each side of the crown. The cingulum is better developed and more basally placed on the labial side than on the other. Moreover, the lingual cingulum is arched apically and thicker posteriorly. The presence of a two-faced asymmetrical cingulum is a common feature among nodosaurids, e.g., *Sauropelta* (Ostrom, 1970) and *Edmontonia* (Carpenter, 1990). The cingula are more nearly symmetrical in *Minmi*, with one only slightly more basal than the other, and the lingual cingulum lacks the arch seen here. On the lingual side of the crown there are a set of small ridges (or sulci) that do not correspond with the denticles, but extend from the bases of the denticles to the cingulum, and may be continuous with the vertical wrinkles of the cingulum. There seem to be slight ridges on the labial side as well that are continuous with the denticles, but these extend only a short distance below them, and do not extend across the entire crown. The pattern of

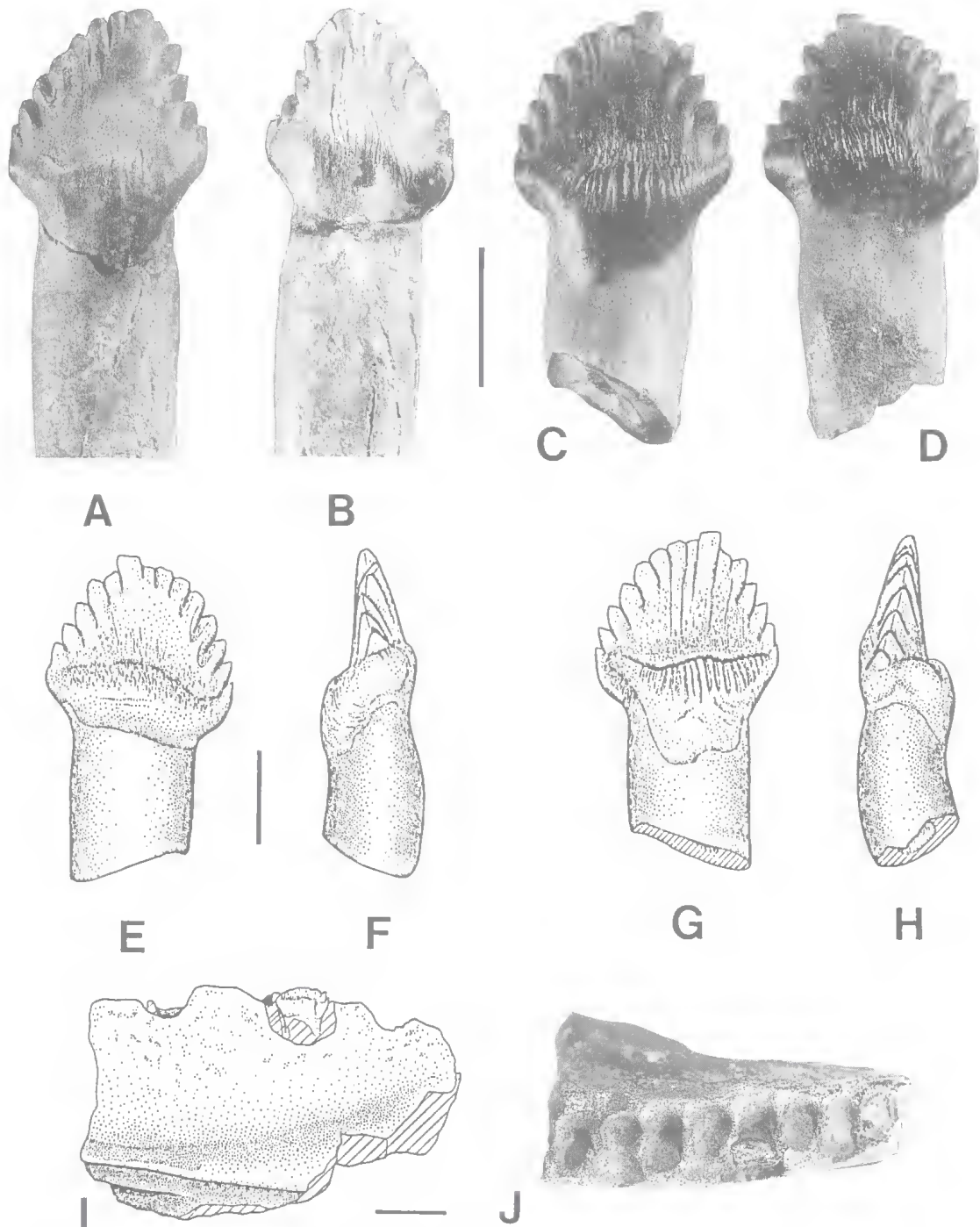


FIG. 1. MLP 86-X-28-1, ankylosaur cranial remains from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. A, C, two teeth in labial view; and B, D, lingual view; scale = 5mm (4x). E, tooth in lingual view; F, distal; G, labial; and H, mesial views; scale = 5mm. I, Left dentary with a tooth in situ in medial view; scale 10mm; and J, in occlusal view.

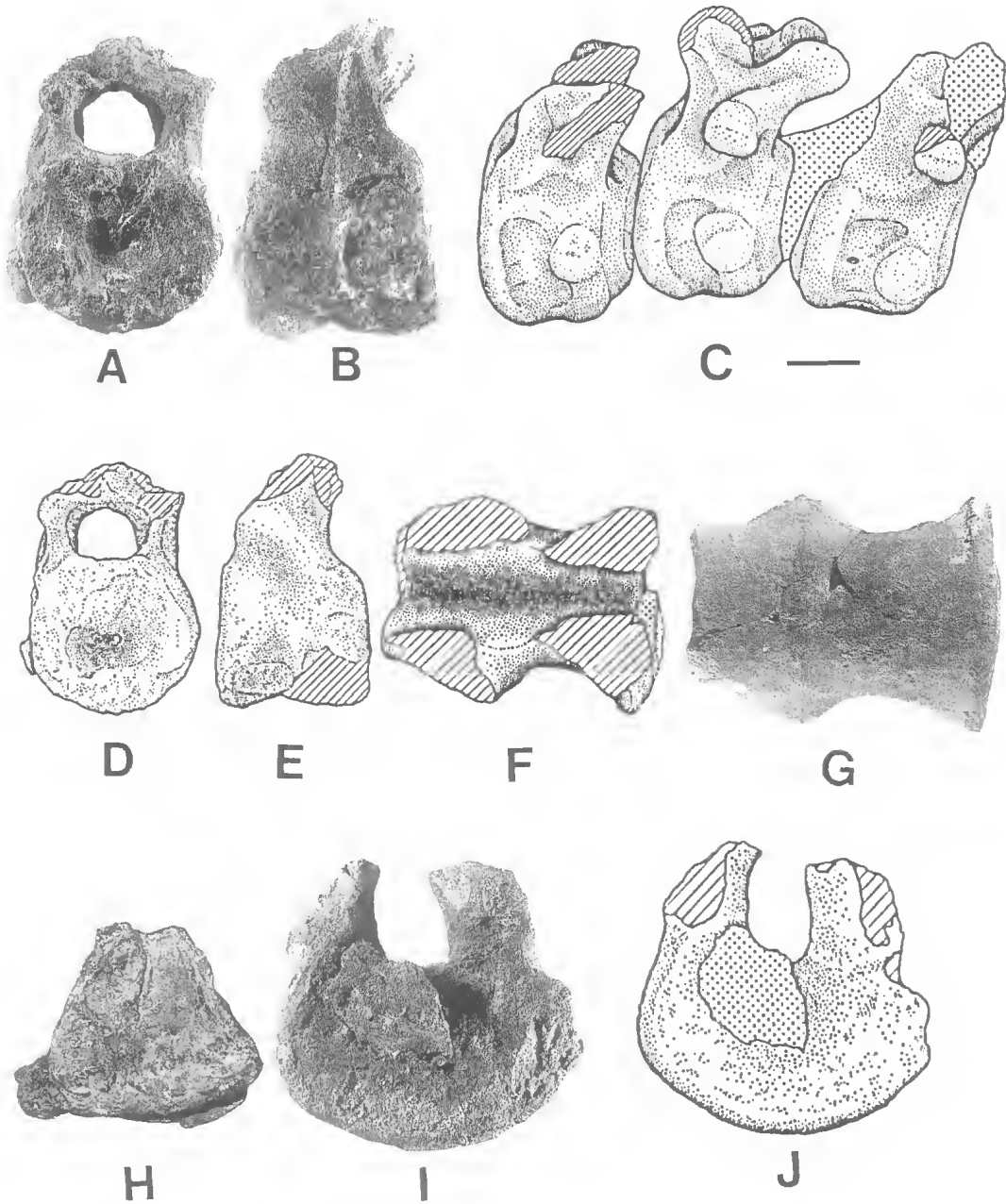


FIG. 2. MLP 86-X-28-1, ankylosaur vertebrae from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. A, D, anterior cervical vertebra in anterior view; and B, E, left lateral view. C, Latex cast from a mould of three articulated vertebrae in right lateral view (0.67x). F, two fused dorsal vertebrae from the ?presacral rod in dorsal view; G, ventral; and I, J, anterior views. H, Caudal vertebra in anterior view. Scale = 20mm.

vertical ridges on the crown is different from that of *Edmontonia*. In the latter, the ridges are continuous with the denticles, i.e., at the margin of the crown the ridges terminate in denticles

(Coombs, 1990; Coombs & Maryanska, 1990). The root is slightly incurved and lingually convex in anterior and posterior views. It is separated from the crown by a slight constriction. If the

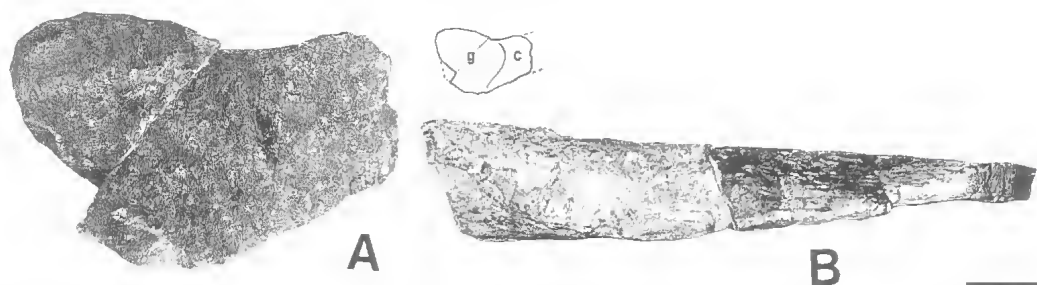


FIG. 3. MLP 86-X-28-1, ankylosaur limb girdle remains from the Late Cretaceous (Campanian) of the James Ross Island, Antarctic Peninsula. A, Scapula in articular (ventral) view. The inset indicates the humeral (g) and coracoid (c) articular surfaces. Medial is to the top. B, Ilium in lateral view. Scale = 20mm.

teeth belong to the lower jaw, they come from the left dentary (it is likely that they belong to the same individual).

Vertebrae and ribs (Fig. 2). About twelve more or less fragmentary vertebrae have been recognised. Most are quite damaged and shattered. A latex cast was made from a mould of three articulated cervical vertebrae (Fig. 2C). These vertebrae are small, with a total length of the series of about 123mm. The fusion of the neural archs to the centra suggests that they do not belong to a juvenile individual. The best preserved vertebra consists of part of the centrum, neural arch pedicles, transverse processes, prezygapophyses and the base of the neural spine. The centra are slightly amphicoelous, wider than long, and high as is common in ankylosaurs (Coombs & Maryanska, 1990). The parapophyses are placed near the anterior border, at mid-height of the centrum in the first preserved vertebra and become moderately higher in those further back. The neural canal is circular to slightly oval, and its diameter reaches a third of the width of the centrum. The transverse processes are short and oriented almost horizontally. The prezygapophyses are well-developed and form an angle with each other of about 60°. On the basis of these characters, the vertebrae are interpreted as coming from the middle of the cervical series (see Eaton, 1960).

In addition, an isolated cervical vertebra is known (Fig. 2F-G, 1-J). This vertebra is about the same size or slightly smaller than the articulated cervicals. The centrum is also amphicoelous and wider than long. The neural canal is broader than high anteriorly, but higher than broad posteriorly. The parapophyses appear to be on the lower half of the lateral side. This suggests that the vertebra comes from the anterior half of the neck and was possibly situated anterior to the articulated series. The cervicals are similar to those of *Minmi*, but

differ in detail. The pedicles of the neural arches seem anteroposteriorly thinner in *Minmi*, and the centra are basically amphiplatyan with only slightly concave (or convex) central articular faces.

Two co-ossified centra (Fig. 2F-G) which preserve parts of the neural arches were originally described as sacral vertebrae (Gasparini et al., 1987: pl. 2, fig. 3). However, the neural canal of the vertebrae, as exposed dorsally, seems to be very narrow for the sacral region. In addition, the centra are only slightly compressed dorsoventrally and there is no fusion of the diapophyses and parapophyses lateroventrally, as occurs in the sacrals. Accordingly, these vertebrae probably come from the presacral rod, not the sacrum. They are tentatively regarded as the first and second vertebrae from the rod because the articular face of the best preserved centrum shows no trace of fusion with another vertebra. Vertebrae from the front of the presacral rod of *Minmi paravertebra* (QM F10329) differ in having a neural canal that is less laterally compressed, but centra that more compressed.

On the other hand, the other fragmentary fused elements may belong to the sacral region. The more complete specimen preserves parts of two possible co-ossified vertebrae, with broken lateral and dorsal attachments. The ventral surface is flat and narrower in the articular region between the elements. The specimen is too fragmentary for accurate identification, but it may be part of the sacral neural arches.

About eight fragments of dorsal ribs are known. The ribs are T-shaped to L-shaped in cross section proximally, a common morphology among ankylosaurs (Coombs, 1978), although found in some other dinosaurs as well.

At least three fragmentary caudal vertebrae are present. One of them contains a centrum with a fragmentary transverse process projecting

ventrolaterally (Fig. 2H), in anterior view this caudal superficially resembles that of a mosasaur. However it is amphicoelous, not procoelous. Two other caudals retain only the lower face of the centrum. A shallow, median groove and articular surfaces for chevrons are visible ventrally. The centra are very short and probably come from the anterior part of the tail. The caudal vertebrae are all similar in size and could belong to the same individual.

Scapula (Fig. 3A). A fragmentary left scapula is the only recognisable part of the pectoral girdle. It includes the glenoid region but the scapular spine is not preserved. The scapula and coracoid were not co-ossified. This, together with small size of the scapula, suggests that it could belong to an immature individual.

Ilium (Fig. 3B). The pelvic girdle is represented by a fragment of ilium. The specimen shows a slightly sigmoid lateral border. The dorsal surface is convex but the ventral surface is flat. The piece probably comes from the central portion of the preacetabular process of a right ilium which in ankylosaurs — differently to other dinosaurs — is unusually twisted laterally to lie in a horizontal plane (Coombs, 1978; Coombs & Maryanska, 1990).

Metapodials and phalanges (Fig. 4). Four fragmentary metapodials and two phalanges are known. The metapodials are broken and lack proximal articular regions. They are relatively broad and bear massive distal articulations, which are approximately perpendicular to the long axis of the shaft (Fig. 4A-B). The moderate robustness of the metapodials suggests that they could belong to the pes rather than to the manus; although in fact, ankylosaurian metatarsals are more slender than metacarpals (Coombs & Maryanska, 1990). Three of the metapodials seem roughly similar in shape but comparatively smaller than metatarsals II, III and IV of the nodosaurid *Sauropelta* (see Ostrom, 1970: pl. 26). The phalanges are very different in form. One is cube-shaped, slightly asymmetrical in ventral view, and longer than wide (Fig. 4C). It probably comes from digit I. The other is a very short, disc-like bone (Fig. 4D). It is tentatively identified as the second phalanx of digit II or III. The disc-like phalanx is about 1.5 times as wide as the other. This difference in size can be interpreted in two ways: either one phalanx was from the manus and the other from the pes, or they are from two different individuals.

Armour (Fig. 5). Dermal elements are represented by five different types (Gasparini et al.,

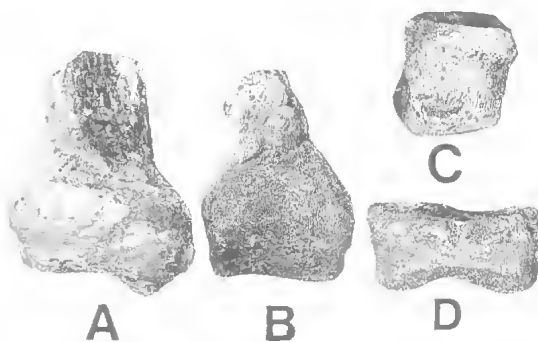


FIG. 4. MLP 86-X-28-1, ankylosaur manual or pedal remains from the Late Cretaceous (Campanian) of the James Ross Island, Antarctic Peninsula. A, B, two metapodials; and C, D, two phalanges in anterior view. Scale = 20mm.

1987): a) keeled, hollow-based scutes; b) massive bulging plates; c) co-ossified flat scutes, overlapping each other; d) oval, low-keeled scutes; and e) tiny button-like ossicles.

Several fragmentary plates of the first type (a) are known. These are massive, with an irregular dorsal surface and prominent keel. Ventrally, the surface is deeply hollowed in the largest preserved specimen (Olivero et al. 1991, fig. 2c). These plates were originally regarded as cranial ossifications and so tentatively referred to the Ankylosauridae (Gasparini et al., 1987). The specimens are too fragmentary to confirm this. The occurrence of prominent lateral horny plates on the skull roof is a conspicuous character of ankylosaurids (Maryanska, 1977; Coombs & Maryanska, 1990) but similar structures could be sporadically present in nodosaurids (Kirkland, pers. comm., 1995).

The second type (b) of armour consists of large, rough-surfaced plates (Gasparini et al., 1987, pl. I, fig. 6; Olivero et al., 1991, fig. 2d). The dorsal surface is sculptured with numerous small pits and rugosities. The ventral face is irregular and hollowed. These plates were originally interpreted as a possible tail-club but there is no direct evidence (i.e. fusion to distal caudal vertebrae) confirming this.

The third kind (c) of armour consists of co-ossified flat scutes overlapping each other and enclosed by small polygonal ossicles (Fig. 5C-D: Gasparini et al., 1987, pl. II, fig. 4). The scutes are subcircular to oval in form, irregular in outline and devoid of a dorsal keel. This pattern resembles that of the sacral armour of *Polacanthus*-like nodosaurids, which are characterised by the fusion of a mosaic of plates into a rigid shield

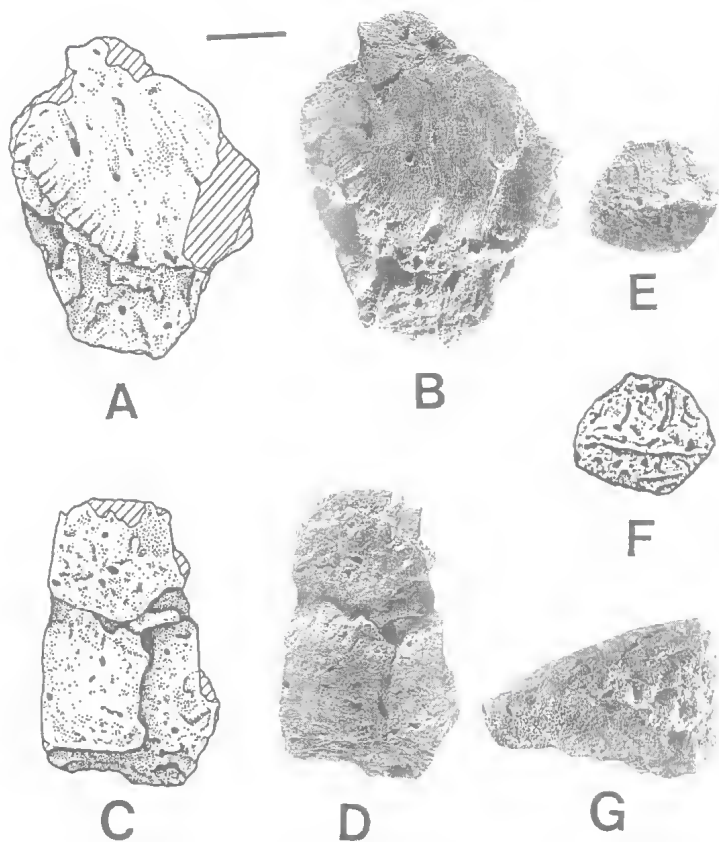


FIG. 5. MLP 86-X-28-1, ankylosaur dermal plates from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. Osteoderms, including A-D, overlapped flat plates; and E, F, an oval low-keeled scute in dorsal view. G, skull roof ossification? Scale = 20mm (0.5x).

(Hulke, 1888; Kirkland & Carpenter, 1994; Pereda-Suberbiola, 1994). As far as known, a synsacral shield could be present in the Antarctic ankylosaur but further material is need to confirm it.

The small to medium-sized scutes (d) are oval in shape and bear a low dorsal keel (Fig. 5E-F: Gasparini et al., 1987, pl. II, fig. 5). They were probably situated in longitudinal rows on the body, as diagnostic for thyreophorans (Sereno, 1986). The ventral surfaces of the scutes are generally flat as in nodosaurids (Coombs, 1978). Together with small ossicles, one of these scutes has been preserved associated with a dorsal rib and ossified tendons (Gasparini et al., 1987, pl. I, figs 3,4). This suggests that the small scutes were arranged in an intercostal position along the trunk, as in *Minmi* and generally among ankylosaurs.

Finally, there are numerous polygonal ossicles (e) of very small size, less than 4mm in diameter

(Gasparini et al., 1987, pl. II, fig. 6). These ossicles probably floated in the skin and formed a continuous pavement between the large dermal elements permitting supple movements of the body (Carpenter, 1984). A histological study of these ossicles is currently in progress (de Ricqlés and collaborators, in preparation).

The new specimen of *Minmi* (QM F18101) also shows five types of dermal armor, but only two of them (types d and e given here) clearly match those of the James Ross Island ankylosaur. These kinds seem to be found in many ankylosaurian taxa. *Minmi* clearly lacked *Polacanthus*-like sacral armor, and had larger (5-6mm diameter) dermal ossicles.

DISCUSSION

The general morphology of the lower jaw, teeth, vertebrae, ilium and armour allow confident attribution of the dinosaur from James Ross Island to the Ankylosauria. At least three derived characters of ankylosaurs (Sereno 1986; Coombs & Maryanska 1990)

are present: posterior dorsal vertebrae fused to form a presacral rod, ilium rotated into the horizontal plane, and body covered by a mosaic of armour plates of several shapes.

In a preliminary account, Gasparini et al. (1987) tentatively assigned the material to the family Ankylosauridae on the following characters: skull co-ossifications with lateral projections, teeth with cingula, and tail-club. However, our redescription of the material advises caution in regard to these features. In fact, on the basis of tooth form the ankylosaurian remains from the Antarctic Peninsula look more likely to be nodosaurid than ankylosaurid. Coombs & Maryanska (1990) pointed out that the two families can usually be distinguished on dental features. These authors cited several characters that are useful in this regard, e.g., conspicuous basal cingulum, cingulum typically higher on the

TABLE 1. Gondwanan ankylosaurs.

TAXON	AGE	PROVENANCE
Nodosauridae indet. (Coria, 1994)	Campanian-Maastrichtian	Patagonia, Argentina
Nodosauridae indet. (Molnar & Wiffen, 1994)	Campanian-Maastrichtian	North Island, New Zealand
Nodosauridae indet. (this paper; Gasparini et al., 1987; Olivero et al., 1991)	Campanian	James Ross I., Antarctic Peninsula
<i>Minmi paravertebra</i> Molnar, 1980 (Molnar, 1980, 1991, this volume; Molnar & Frey, 1987)	Aptian-Albian	Queensland, Australia
Ankylosauria indet. (Rich & Rich, 1989)	Aptian-Albian	Victoria, Australia
Ankylosauria (Chatterjee & Rudra, this volume)	Maastrichtian	Gujarat, India

lingual face, and grooves on crown generally better developed (Coombs & Maryanska, 1990). All of these features are present in the teeth from James Ross Island and this suggests that they belong to a nodosaurid ankylosaur. The differences in tooth form and the absence of a sacral 'buckler' in *Minmi* are the clearest distinctions between the Antarctic beast and *Minmi*. Thus they seem not to be closely related — insofar as we can tell when many corresponding elements are either missing (in the Antarctic specimen) or not yet exposed (in *Minmi*). The currently-known material from James Ross Island is too fragmentary for generic or specific identification and is here provisionally referred to Nodosauridae indet. Further material is needed to accurately define the affinities of the Antarctic ankylosaur.

The geologists who discovered the material thought it derived from a single partial skeleton of small size (Olivero, pers. comm.). Only some of the bone fragments were recovered because the ice was very thick around the fossils and the bones were broken by frost action. However, revision of the material at La Plata raised the possibility that two individuals were represented. Thus size differences between some of the bones, e.g., phalanges, would be accounted for. Also, on the one hand the neural arches are fused to the centra, which supports the idea that the vertebrae do not belong to a juvenile. But, on the other, the scapula and coracoid (not found) were not fused, in contrast to the usual condition of adult ankylosaurs (Coombs & Maryanska, 1990). Nonetheless these conditions are both seen in the skeleton of *Minmi* (QM F18101) which clearly derives from a single (articulated) individual. The differences in size between the phalanges may be due to one being manual and the other pedal. So there is no strong evidence that two individuals are represented.

The absence of fusion of the scapula to the coracoid suggests immaturity, although fusion does not take place in *Hylaeosaurus* (Pereda-

Suberbiola, 1993) nor *Edmontonia* (Carpenter, 1990). So the absence of fusion of the splenial and dentary is perhaps more convincing. Fusion of the neural arches to the centra indicates that the animal was not very young. So most of the skeletal remains from James Ross Island are tentatively regarded as those of an immature, small individual. The estimated body length of the Antarctic ankylosaur is 3 or 4m.

PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

Ankylosaurs were quadrupedal, armoured dinosaurs that lived from the Middle Jurassic to the Late Cretaceous (Coombs & Maryanska, 1990). The distribution of the two families is probably vicariant. The more conservative Nodosauridae are known in Europe from the Callovian to the Maastrichtian (Galton, 1983; Pereda-Suberbiola, 1992), and in North America from the Tithonian to the Maastrichtian (Carpenter & Breithaupt, 1986; Kirkland & Carpenter, 1994). The club-tailed Ankylosauridae are present in Asia from the Bathonian-Callovian to the Maastrichtian (Maryanska, 1977; Dong, 1993), and in North America during Campanian-Maastrichtian times (Coombs, 1986).

Unquestionable ankylosaurs from Gondwanaland include discoveries from the Lower Cretaceous of Australia and from the Late Cretaceous of New Zealand, South America and Antarctica (Table 1). Chatterjee & Rudra (this volume) also report an ankylosaur from India. In Australia, there are five Aptian-Albian occurrences in Queensland, including the holotype of *Minmi paravertebra* (Molnar, 1980; Molnar & Frey 1987) and a nearly complete, articulated skeleton referable to *Minmi* (Molnar, 1991, this volume), and two occurrences in Victoria (Rich & Rich, 1989). Ankylosaurs are also present in the Campanian-Maastrichtian of North Island, New Zealand (Molnar & Wiffen, 1994) and that

TABLE 2. Specimens from Gondwanaland incorrectly referred to the Ankylosauria.

TAXON	AGE	PROVENANCE	STATUS
<i>Loricosaurus scutatus</i> Huene 1929 (Huene, 1929)	Maastrichtian	Argentina	Titanosaurid sauropod (Powell, 1980; Bonaparte & Powell, 1980)
<i>Lametasaurus indicus</i> Matley 1923 (Matley, 1923; Huene & Matley, 1933)	Maastrichtian	India	Composiite theropod, sauropod and crocodilan (Chakravarti, 1935; Walker, 1964, Molnar & Frey, 1987)
<i>Brachypodosaurus gravis</i> Chakravarti 1934 (Chakravarti, 1934)	Maastrichtian	India	Stegosaur? (Galton, 1981)
<i>Stegosaurus madagascariensis</i> Piveteau 1923 (Piveteau, 1923; Russell et al., 1976)	Campanian	Madagascar	unknown
Acanthopholidae indet (Lapparent, 1960)	Albian	Niger	Stegosaur? (Molnar & Frey, 1980; X. Pereda-S., pers. obs.)

of Río Negro Province, Patagonia, Argentina (Coria, 1994; Salgado & Coria, in press). The list is completed with these remains from the Campanian of the Antarctic Peninsula (Gasparini et al., 1987; Olivero et al., 1991).

Ankylosaurs have also previously been reported from the Early Cretaceous of North Africa (Lapparent, 1960) and the Late Cretaceous of India (Matley, 1923; Huene & Matley, 1933; Chakravarti, 1934; Coombs, 1978) and Madagascar (Piveteau, 1923; Russell et al., 1976). Nevertheless, these remains are probably not ankylosaurian and can be assigned to other groups of dinosaurs or archosaurs (Table 2; see Molnar & Frey, 1987, for a discussion). As far as known, no conclusive evidence confirms the occurrence of ankylosaurs in Africa (Molnar & Frey, 1987; X. P.-S., pers. obs.), India (Chakravarti, 1935; Walker, 1964; Galton, 1981; Molnar & Frey, 1987) other than that reported by Chatterjee & Rudra, nor Madagascar (Sues, 1980). Dermal scutes from Argentina (*Loricosaurus scutatus* Huene, 1929) have been removed from the ankylosaurs to the titanosaurid sauropods (Powell, 1980; Bonaparte & Powell, 1980).

The presence of ankylosaurs in Antarctica during the Late Cretaceous can be explained as the result of dispersal from the northern continents to southern Gondwana (see discussion in Gasparini et al., 1987; Olivero et al., 1991). The time of this passage is not well known but two hypotheses may be considered:

First, an early migration during the Late Jurassic via Africa or South America. At this time, nodosaurids were present in Europe and North America and palaeobiogeographical evidence shows that passage to Gondwanaland was possible (Galton, 1977). If so, ankylosaurs were present in southern continents before the breakup

of Gondwana (Bonaparte 1986). According to Molnar (1980, 1991, this volume), the mixture of primitive and specialised characters in *Minmi* could be the result of endemic evolution (because of geographical isolation) of this lineage of ankylosaurs in Australia during the Early Cretaceous. There is no evidence of Jurassic ankylosaurs in Gondwanaland and there seems no close affinity between the Antarctic ankylosaur and *Minmi*. On the other hand, the Late Cretaceous polar dinosaur fauna from New Zealand, that includes an ankylosaur, has been interpreted as probably representative of the terrestrial assemblages that inhabited Late Cretaceous Antarctica (Molnar & Wiffen, 1994). Unfortunately, a comparison between the Antarctic ankylosaur and that from New Zealand is not possible with the available material.

Second, a late dispersal, during the Late Cretaceous, via South America. The vertebrate interchange between North America and South America in the Campanian is well documented (Bonaparte, 1986; Gayet et al., 1992). Ankylosaurs could have traversed South America and reach Antarctica. This hypothesis is supported by the presence of a nodosaurid in Patagonia at this time (Coria, 1994; Salgado & Coria, in press). A continuous or intermittent land connection between Antarctica and South America is likely for some period during the Late Cretaceous (Olivero et al., 1991) and the Early Paleogene (Woodburne & Zinsmeister, 1984; Gasparini et al., 1986; Marensi et al., 1994).

The occurrence of an armoured dinosaur in the Antarctic Peninsula is also interesting because it is one of the rare occurrences of ankylosaurs in high latitudes. During the Late Cretaceous, the Antarctic Peninsula was situated near its present position, at about 64°S (Zinsmeister, 1987). Other reports of ankylosaurs in high palaeo-

latitudes are of the nodosaurid *Edmontonia* from the Late Cretaceous of Alaska (Gangloff, 1995) at about 70°N, *Minmi* from the uppermost Early Cretaceous of Australia (Molnar, 1980, 1991, this volume) between 70° and 80°S (Veevers et al., 1991), and an indeterminate ankylosaur from the Late Cretaceous of New Zealand (Molnar & Wiffen, 1994) at least 66°S (see Barron, 1986 and Veevers et al., 1991, for palaeogeographical maps). In addition to the occurrence of the Antarctic ankylosaur in high latitudes, there is independent evidence of a diversified flora suggesting a rather mild climate and a relatively high humidity, at least in the area where the dinosaur remains were found (Baldoni, 1992).

As noted by Molnar & Wiffen (1994), although large ankylosaurs (up to 9m) are known from both Asia and North America, there is no indication of any from the Gondwanan continents more than 4m long, including Australia, New Zealand, Antarctica, and South America. With the exception of the latter find, all the others probably represent components of insular, near-polar faunas.

Finally, the ankylosaur remains from James Ross Island were recovered from shallow marine deposits associated with marine invertebrates (Olivero et al., 1991). It should be noted that among ankylosaurs, ankylosaurid specimens are known only from continental deposits (Table 22.1 of Coombs & Maryanska, 1990) although articulated nodosaurid bones have (occasionally) been reported from marine formations (Horner, 1979; Carpenter et al., 1995; Coombs & Deméré, 1996). In addition there have been several recent discoveries of disarticulated nodosaurid specimens in marine formations as well (Coombs, 1995; Gangloff, 1995; Holden, 1996; Lee, 1996). This taphonomic difference suggests that by the Late Cretaceous nodosaurids preferred nearshore environments, whereas ankylosaurids probably lived in more inland habitats. A similar ecological segregation has been suggested among hadrosaurid dinosaurs (Horner, 1979; Carpenter et al., 1995). Walter Coombs (pers. comm., 1996) pointed out that recent discoveries of specimens from southern California (Coombs & Deméré, 1996), Alaska (Gangloff, 1995) and, reportedly, Hokkaido (Holden, 1996) suggest a circum-Pacific distribution of nodosaurids, reminiscent of that of desmostylians. He also noted that the Alaskan specimen (referred to *Edmontonia* sp.) is a skull very like that of ROM 1215 from the continental Campanian of Alberta. This suggests that nodosaurids were not restricted to marginal marine habitats — and nodosaurids show no an-

kylosaurid features in their morphology — but perhaps had a broader tolerance of habitats than ankylosaurids. To sum up, the Antarctic ankylosaur remains were found in shallow marine sediments and in high palaeolatitudes, a typical condition among nodosaurids but unknown in ankylosaurids. This indirectly supports the nodosaurid affinities of the Antarctic dinosaur.

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LITERATURE CITED

- BALDONI, A. 1992. Palinología de la Formación Santa Marta, Cretácico superior de la Isla James Ross, Antártida. Pp. 359-374. In Rinaldi, C. (ed.) 'Geología de la Isla James Ross'. (Instituto Antártico Argentino, Buenos Aires).
- BARRON, E.J. 1986. Global Cretaceous Paleogeography – International Geologic Correlation Program Project 191. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 207-214.
- BONAPARTE, J.F. 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. *Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza* 2: 63-95.
- BONAPARTE, J.F. & POWELL, J.E. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mémoires de la Société géologique de France* 139: 19-28.
- CARPENTER, K. 1984. Skeletal reconstruction and life restoration of *Sauropelta* (Ankylosauria: Nodosauridae) from the Cretaceous of North America. *Canadian Journal of Earth Sciences* 21: 1491-1498.
1990. Ankylosaurs systematics: example using *Panoplosaurus* and *Edmontonia* (Ankylosauria: Nodosauridae). Pp. 281-298. In Carpenter, K. & Currie, P.J. (eds) 'Dinosaur Systematics: Perspectives and Approaches'. (Cambridge University Press: Cambridge).
- CARPENTER, K. & BREITHAUPT, B. 1986. Latest Cretaceous occurrences of nodosaurid ankylosaurs (Dinosauria: Ornithischia) in western North America and the gradual extinction of the

- dinosaurs. *Journal of Vertebrate Paleontology* 6: 251-257.
- CARPENTER, K., DILKES, D. & WEISHAMPEL, D.B. 1995. The dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas). *Journal of Vertebrate Paleontology* 15: 275-297.
- CHAKRAVARTI, D.K. 1934. On a stegosaurian humerus from the Lameta beds of Jubbulpore. *Journal of the Geological, Mineralogical and Metallurgical Society of India* 6: 75-79.
1935. Is *Lametasaurus* an armoured dinosaur? *American Journal of Science* 30: 138-141.
- CHATTERJEE, S. & RUDRA, D.K. 1996, this volume. KT events in India: impact, rifting, volcanism and dinosaur extinction. *Memoirs of the Queensland Museum* 39(3): 489-532.
- COOMBS, W.P., Jr 1978. The families of the ornithischian dinosaur order Ankylosauria. *Palaentology* 21: 143-170.
1986. A juvenile ankylosaur referable to the genus *Euoplocephalus* (Reptilia, Ornithischia). *Journal of Vertebrate Paleontology* 6: 162-173.
1990. Teeth and taxonomy in ankylosaurs. Pp. 269-279. In Carpenter, K. & Curric, P.J. (eds) 'Dinosaur Systematics: Perspectives and Approaches'. (Cambridge University Press: Cambridge).
1995. A nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Lower Cretaceous of Texas. *Journal of Vertebrate Paleontology* 15: 298-312.
- COOMBS, W.P., Jr & DEMERE, T.A. 1996. A Late Cretaceous nodosaurid ankylosaur (Dinosauria: Ornithischia) from marine sediments of coastal California. *Journal of Paleontology*, 70: 311-326.
- COOMBS, W.P., Jr & MARYANSKA, T. 1990. Ankylosauria. Pp. 456-483. In Weishampel, D.B., Dodson, P. & Osmólska, H. (eds) 'The Dinosauria'. (University California Press: Berkeley).
- CORIA, R.A. 1994. Sobre la presencia de dinosaurios ornitisquios acorazados en Sudamérica. *Ameghiniana* 31: 398.
- DONG, Z. 1993. An Ankylosaur (ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. *Vertebrata Palasiatica* 20: 83-87.
- EATON, T. 1960. A new armored dinosaur from the Cretaceous of Kansas. *University of Kansas, Paleontological Contributions* 8: 1-24. CHECK
- GALTON, P.M. 1977. The ornithopod *Dryosaurus* and a Laurasia - Gondwanaland connection in the Upper Jurassic. *Nature* 268: 230-232.
1981. *Craterosaurus pottonensis* Seeley, a stegosaurian dinosaur from the Lower Cretaceous of England, and a review of Cretaceous stegosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 161: 28-46.
1983. Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of England. *Palaentographica A* 182: 1-25.
- GANGLOFF, R.A. 1995. *Edmontonia* sp., the first record of an ankylosaur from Alaska. *Journal of Vertebrate Paleontology* 15: 195-200.
- GASPARINI, Z., FUENTE, M. de la & DONADIO, O. 1986. Los reptiles cenozoicos de la Argentina. Implicancias paleoambientales y evolución biogeográfica. *Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza* 2: 119-130.
- GASPARINI, Z., OLIVERO, E., SCASSO, R. & RINALDI, C. 1987. Un ankylosaurio (Reptilia, Ornithischia) campaniano en el continente antártico. *Anais X Congr. Brasi. Paleont. Rio de Janeiro* 1987: 131-141. CHECK
- GAYET, M., RAGE, J.-C., SEMPERE, T. & GAGNIER, P.-Y. 1992. Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. *Bulletin de la Société géologique de France*, 163: 781-791.
- HAMMER, W.R. & HICKERSON, W.J. 1994. A Crested Theropod Dinosaur from Antarctica. *Science* 264: 828-830.
- HOLDEN, C. 1996. On the dinosaur trail. *Science*, 271: 1061,1063.
- HOOKE, J.J., MILNER, A.C. & SEQUEIRA, S. 1991. An ornithopod dinosaur from the Late Cretaceous of West Antarctica. *Antarctic Science* 3: 331-332.
- HORNER, J.R. 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-central Montana with a checklist of Upper Cretaceous dinosaur remains from marine sediments in North America. *Journal of Paleontology*, 53: 566-577.
- HUENE, F. von 1929. Los saurisquios y ornitisquios del Cretáceo argentino. *Anales de la Museo de La Plata, ser. Paleont.* 3: 1-196.
- HUENE, F. von & MATLEY, C.A. 1933. The Cretaceous Saurischia and Ornithischia of the Central Provinces of India. *Memoirs of the Geological Survey of India, Paleontologia Indica* 21: 1-74.
- HULKE, J.W. 1888. Supplemental note on *Polacanthus foxii*, describing the dorsal shield and some parts of the endoskeleton, imperfectly known in 1881. *Philosophical Transactions of the Royal Society of London* 178: 169-172.
- KIRKLAND, J.I. & CARPENTER, K. 1994. North America's First Pre-Cretaceous Ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of Western Colorado. *Brigham Young University Geological Studies* 40: 25-42.
- LAPPARENT, A.F. de 1960. Les Dinosauriens du 'Continental intercalaire' du Sahara central. *Mémoires de la Société géologique de France* 88A: 1-57.
- LEE, Y.-N. 1996. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw Formation (Late Albian) of Texas. *Journal of Vertebrate Paleontology* 16: 232-245.
- MARENSSI, S., REGUERO, M., SANTILLANA, S. & VIZCAINO, S. 1994. Eocene land mammals

- from Seymour Island, Antarctica: palaeobiogeographical implications. *Antarctic Science* 6: 3-15.
- MARYANSKA, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Paleontologia Polonica* 37: 85-151.
- MATLEY, C.A. 1923. Note on an armoured dinosaur from the Lameta Beds of Jubbulpore. *Records of the Geological Survey of India* 55: 105-109.
- MILNER, A.C., HOOKER, J.J. & SEQUEIRA, S. 1992. An ornithopod dinosaur from the Upper Cretaceous of the Antarctic peninsula. *Journal of Vertebrate Paleontology* 12 (suppl. to 3): 44A. (abstract)
- MOLNAR, R.E. 1980. An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum* 20: 77-87.
1991. A nearly complete articulated ankylosaur from Queensland, Australia. *Journal of Vertebrate Paleontology* 11 (suppl. to 3): 47A. (abstract)
- 1996, this volume. Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. *Memoirs of the Queensland Museum* 39(3): 653-668.
- MOLNAR, R.E. & FREY, E. 1987. The paravertebral elements of the Australian Ankylosaur *Minmi* (Reptilia: Ornithischia, Cretaceous). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175: 19-37.
- MOLNAR, R.E., LOPEZ ANGRIMAN, A. & GASPARINI, Z. 1996, this volume. An Antarctic Cretaceous theropod. *Memoirs of the Queensland Museum* 39(3):669-674.
- MOLNAR, R.E. & WIFFEN, J. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretaceous Research* 15: 689-706.
- OLIVERO, E. 1992. Asociaciones de amonites de la Formación Santa Marta (Cretácico tardío), Isla James Ross. Pp. 47-75. In Rinaldi, C. (ed.) 'Geología de la Isla James Ross'. (Instituto Antártico Argentino: Buenos Aires).
- OLIVERO, E., GASPARINI, Z., RINALDI, C. & SCASSO, R. 1990. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical implications. Pp. 617-622. In Thomson, M.R.A., Crame, J.A. & Thomson, J.W. (eds) 'Geological Evolution of Antarctica'. (Cambridge University Press: Cambridge).
- OSTROM, J.H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Bulletin, Peabody Museum of Natural History* 35: 1-234.
- PEREDA-SUBERBIOLA, X. 1992. A revised census of European Late Cretaceous nodosaurids (Ornithischia: Ankylosauria): last occurrence and possible extinction scenarios. *Terra Nova* 4: 641-648.
1993. *Hylaeosaurus*, *Polacanthus*, and the systematics and stratigraphy of Wealden armoured dinosaurs. *Geological Magazine* 130: 767-781.
1994. *Polacanthus* (Ornithischia, Ankylosauria), a transatlantic armoured dinosaur from the Early Cretaceous of Europe and North America. *Palaeontographica A* 232: 133-159.
- PIVETEAU, J. 1923. Contribution à l'étude des formations lagunaires du Nord-Ouest de Madagascar. *Bulletin de la Société géologique de France* 26: 33-38.
- POWELL, J.E. 1980. Sobre la presencia de una armadura dérmica en algunos dinosaurios titanosáuridos. *Acta Geologica Lilloana* 15: 41-47.
- RICH, T.H.V. & RICH, P.V. 1989. Polar dinosaur and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5: 15-53.
- RUSSELL, D., RUSSELL, D., TAQUET, P. & THOMAS, H. 1976. Nouvelles récoltes de Vertébrés dans les terrains continentaux de la région de Majunga (Madagascar). *Comptes Rendus sommaire de la Société géologique de France* 5: 204-208.
- SALGADO, L. & CORIA, R.A. in press. First evidence of an armoured ornithischian dinosaur in the Late Cretaceous of North Patagonia, Argentina. *Ameghiniana*.
- SERENO, P.C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* 2: 234-256.
- SUES, H.-D. 1980. A pachycephalosaurid dinosaur from the Upper Cretaceous of Madagascar and its paleobiogeographical implications. *Journal of Paleontology* 54: 954-962.
- VEEVERS, J.J., POWELL, M.C.A., & ROOTS, S.R. 1991. Review of seafloor spreading around Australia. I. Synthesis of the patterns and spreading. *Australian Journal of Earth Sciences* 38:373-389.
- WALKER, A.D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society London B* 248: 53-134.
- WOODBURNE, M.O. & ZINSMEISTER, W.J. 1984. The first land mammal from Antarctica and its biogeographic implications. *Journal of Paleontology* 58: 913-948.
- ZINSMEISTER, W.J. 1987. Cretaceous paleogeography of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 197-206.